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IX.—*On the Sexual Life of Plants, and Parthenogenesis.* By Dr. H. Karsten, Lecturer on Botany at the University of Berlin*.

[Plates IX. A, X. & XI.]

The experience of past ages, that certain plants only produce fruit and fertile seed when two are grown together, laid the first ground for the doctrine of the sexuality of plants. The Arab writers, about 900 years after Christ, first drew particular attention to the phenomenon, and recognized its analogy to animal nature. The cultivation of the Date-palm, the Pistacio, of the *Carica Papaya*, &c., led observers to the knowledge of the purpose of the pollen and ovules in the development of seeds. But Clusius was the first botanist who pointed out distinctly that those plants of the *Carica Papaya* bearing stamens were the male, whilst, in accordance with the prevalent popular views, he called those which bore the fruit the female.

John Ray, who first remarked the fixed constancy in the number of the carpels (a fact employed at the present day, since the time of Jussieu, as the basis of the natural classification of the vegetable kingdom), arrived, after numerous experiments and observations, at the conclusion that the anthers of male plants were indispensable to the female in the production of germs.

The scientific foundation of the doctrine of the sexuality of plants was further advanced by our distinguished fellow-countryman, Rudolph Jacob Camerarius, Professor in Tübingen. Camerarius supplied by his researches the groundwork for that first logically-contrived system of plants which, thirty years later, Linnæus gave to his contemporaries.

* Translated by J. T. Arlidge, A.B., M.B. &c., from the original memoir communicated by the Author, to whose kindness we are likewise indebted for the use of the original plates.

By the labours of Burkard, Morland, C. J. Geoffroy, Bradley, Vaillant, Blair, and other observers, the sexual relations of plants were in various ways so elucidated, that, to the methodical mind of the great Swedish naturalist, and by means of his own numerous and accurate observations, their proofs were complete and multiplied. Indeed, he clearly proved that the female plants of *Cannabis sativa,* when carefully protected from the access of the pollen, produced no seeds.

The views of Tournefort and Pontedera, based upon some fallacious observations, respecting the importance and purpose of the anthers, failed to invalidate the antagonistic facts adduced by Linnæus and Dillenius.

The researches of Needham (1745) and Gleichen (1781) on the structural relations between the pollen and stigma, as well as the successful attempts of Kölreuter to generate bastard forms by scattering the pollen of other plants on the stigma, contributed most valuable support in favour of the doctrine of the sexuality of plants.

The inexact observations of F. J. Schelver and Henschel were insufficient to cast a suspicion upon the results obtained by Camerarius, Linnæus, Kölreuter, and others.

The hypothesis of the sexuality of plants entered on a new stage as a consequence of the labours of the distinguished anatomists of this century. The elongation of the pollen-cells was first observed by Amici in 1823; and Brongniart subsequently witnessed, in several plants, the prolongation of tubes from the pollen adherent to the stigma, and the extrusion of corresponding tubules from the orifice (mouth) of the ovules. The latter he presumed to be conducting tubes, through which the fructifying contents of the pollen-tubes (for, like Needham, he imagined that these tubes burst within the conducting tissue of the style) were conveyed to the embryonic sac, discovered by Malpighi to be present within the ovules. Amici followed the pollen-tubes, as is illustrated by the communication presented by Mirbel, from the pollen-corpuscle, through the conducting tissue (observed by Malpighi, as early as 1675, in Monocotyledons) of the canal of the style and of the embryo, to that little aperture in the seed (discovered by Grew in 1671), the mouth of the ovule (since named by Turpin the micropyle), into which this conscientious inquirer, moreover, saw it enter. This was confirmatory of the idea started by Samuel Morland (1703), that the pollen descended through the style into the ovary, and there entered the micropyle of the ovules. In this phenomenon we also find the true explanation of the fact recorded by Richard in 1811, that fibres grew from within the ovules of *Blyxa Auberti.*

Robert Brown, between 1831 and 1833, repeated and confirmed, to the fullest extent, the discovery of Amici in the case of the families of Orchidaceæ and Asclepiadaceæ. Amici, besides, very correctly showed that the elongation of the inner coat of the pollen-grains (usually regarded as simply an act of extension) was effected by a process of growth at the expense of the fluid supplied by the surrounding conducting cellular tissue. The end of the pollen-tube in contact with the ovule Schleiden followed and traced into its tissue, and came to the conviction that, in a large number of plants, the primary formation of the embryo takes place in the interior of this intruded sac of the pollen.

Horkel, Wydler, and, in part, Meyen, accepted Schleiden's views; and Schacht, in his extended prize essay sent to the Royal Netherlands Institute, contributed a large number of proofs in support of Schleiden's discovery. Repeated experiments and investigations that I undertook also caused me to side in general with this observer, although I held the opinion of Meyen and Brongniart to be generally true, that only the union of the contents of the two heterogeneous cells—viz. of the pollen-cell and of the embryonic sac—is necessary, according to the osmotic capacity of the membranes concerned (at one time of the pollen tube, at another of the embryonic sac) or through the union of these two histological elements, to give rise to the development of a new individual.

In the mean time, Griffith (in 1835, at Calcutta) saw, in *Santalum album* and in *Osyris*, the outgrowth of the embryonic sac, in the form of a tube of greater or less length, from the naked ovules as far outwards as the funiculus. The development of the plant-germ only proceeded when the pollen-tube entered within this open and freely-exposed cavity of the embryonic sac. On the other hand, in *Viscum* the germ appeared to him to take its origin in the pollen-tube itself.

In 1846, Amici, Mohl, and Hoffmeister pronounced themselves decidedly in favour of the opinion that the germ never originates within the pollen-tube, but by the enlargement of one of the cells floating freely in the fluid of the embryo-sac, after the pollen-tube has so extended itself as to reach to the vicinity of that sac.

Subsequently to these different interpretations as put forward by various able observers, Schleiden suggested the probability that the opinion first advanced by Brongniart might in many cases be true, and that the germ took its rise from the conjugation of the pollen-tube with a pre-existing embryo-vesicle. At the same time the last-named naturalist, and, at a later period, Radlkofer, and, last of all, Schacht, from his observations in

Madeira on *Gladiolus segetum,* advocated the opinion of Amici and Mohl with reference to the production of the embryo, as exclusively correct.

Not one of these anatomists called in question the theory of the sexual origin of plants put forward by Camerarius and Linnæus. Their views differed only on the question whether the rudiments of the new being were commenced exclusively within the embryo-sac, or exclusively within the pollen-tube, or by the united action of the two organs, after the manner of the conjugation of the Confervæ. The majority of botanists certainly incline towards the opinion that the basis of the young embryo is furnished solely by the germinal vesicles contained within the embryo-sac, and never by the pollen-cell, whose contents serve no other purpose than that of its fructification. Moreover, the plants which Linnæus cautiously named Cryptogamia have been of late years for the most part proved to be Phanerogamia; for, in 1848, Suminski, by observations first made on the thalli of Ferns, showed that those organs which Hedwig, in the case of Mosses, had rightly intimated to be anthers and pistils, actually performed the functions of such structures in Ferns; and since then, in 1850, I sent from Venezuela to Prof. Ehrenberg, as Secretary of the Berlin Academy, the first part of the history of the fructification of an Alga, which confirmed the idea of Nägeli respecting the sexual nature of the two sorts of stalked branches remarked by Vaucher. These two observations together made us acquainted with the extreme forms of the fructifying organs among the Cryptogamia: namely, in the one case the motory apparatus, which is to be compared to the extine of the pollen, is developed pre-eminently; in the other case the cell, which is comparable with the intine of the pollen, attains the maximum development. Still, in both cases, the latter is always present as the special fructifying organ—overlooked, it is true, by many observers, either because, in cellular Cryptogamia, they considered it to be an integral part of the spiral fibres producing the motions, or because, in the vascular Cryptogamia, they examined spiral fibres from which the fructifying cells were torn off.

The conjugation of *Spirogyra,* described by Vaucher as the simplest form of a reproductive process, is indeed still so regarded by the majority of botanists at the present day, and my researches on *Vaucheria* show it to be so in the clearest manner. In some cases, the impregnation of the naked archegonium takes place by means of a free spherical cell (Pl. IX. A. fig. 23 *a*), which escapes from the open extremity of the antheridium within which it was produced, adheres to the archegonium, and after a time coalesces with it, so that the two united lay the foundation for the new individual. However, I more frequently observed that "the apex of the archegonium ('separation-cell,' *Absonderungszelle*) is applied to the curved branch—the antheridium, and that the membrane of the latter becomes absorbed at the point of contact, and then the cells existing in it, filled with colourless muco-granular matter, discharge themselves into the 'separation-cell.' Once, indeed, I clearly witnessed (as I have represented in fig. 23 *c*) that in this process the membrane of the 'separation-cell' (archegonium) became thrust inwards, whilst the secreted matter existing in it decreased, to make room for the penetrating cell.

"Whilst it is easy to make out the whole process of fertilization, it is as difficult to answer the question respecting the condition of the membrane of the separation-cell (archegonium) in the natural condition of the plant, without preparation, as that respecting that of the embryo-sac in compound higher plants. I succeeded in making this point clear by allowing the cells found in actual union to dry up, whereby the coloured matters which lined the inner wall of the 'separation-cell' were withdrawn from the extremity which was occupied by the cell that had there penetrated it (Pl. IX. A. fig. 23 *b* & fig. 23 *c*).

"After the act of impregnation is accomplished, the 'separation-cell' (the archegonium) reassumes the same appearance as before, except that, by transmitted light, the newly produced cell appears of a brownish colour in the centre.

"The result of the two different forms of conjugation of the contents of the curved (antheridium) and of the ovate (archegonium) branch-cell is the formation of a similar product: this is the germ of a young plant, which forthwith, or so soon as the necessary conditions are furnished, developes itself into a simple or very slightly branched cylinder. If the plant, for instance, after impregnation has been accomplished, be moistened only just so much as is necessary to prevent its being quite dried up, the germs formed are not developed, its contents lose colour throughout, and at the same time its enveloping membrane grows thicker. I have kept such germs under observation for three months together. On the contrary, when placed in water, they become green again, and develope into long fibres."

I have here detailed my observations thus fully, in order that they may be compared with the quotations from them given by Pringsheim, through which various more recent authors, who have not given themselves the trouble to refer to the original statements, have been led into error. Pringsheim, who confessedly was unacquainted with the plants examined by me in the colony of Tovar, in Caracas, though he investigated other very similar plants, says, when citing my remarks:—

"In the first place, the extremities of the mother-spore-cells apply themselves laterally to the little protuberances (corniculi), whereupon the membrane of the latter at these lateral points becomes pierced through, and the 'Karsten'-cells are transferred through these apertures from the protuberances to the mother-spore-cells.

"This is the description of the process advanced by Karsten; and I can only express it as my opinion that the explanation given by that naturalist of this account rests upon a false interpretation of what he has seen.

"An aperture never exists on the sides of the projections*. In the instance figured by Karsten, the protuberance (little horn) is in contact, as happens perhaps as frequently as not, with the mother-spore-cell; but the protuberance is shown to be here quite entire and closed below, and nothing whatever is extruded from it; in fact, Karsten's figure represents it replete with contents, and conveys a more truthful impression than his explanation of it."

Pringsheim in this place copies my figure (23 *c*); but he prudently omits fig. 23 *b*, which exhibits the emptied antheridium, and would of itself furnish a contradiction to his denial of my statements †. It has been the fate of Pringsheim himself, who subsequently carried out some researches on the reproduction of *Œdogonium*, *Bulbochæte*, and *Saprolegnia*, to be compelled to confirm my views relative to *Vaucheria* by analogies which he discovered in *Saprolegnia*. He, moreover, discovered in *Saprolegnia* (supposing Pringsheim's account of his own researches to be more credible than his extracts from the writings of others) a similar double process of reproduction,—in the one case by the intermingling of the heterogeneous contents of two adjoining branches (compare the conjugation and the above delineation of the fertilization of *Vaucheria* and fig. 23), and, in the second case, a mode of fructification corresponding with that of the higher Cryptogamia, viz. by cells provided with locomotive cilia.

That the act of fertilization may be accomplished in other Algæ allied to *Vaucheria* by means of cells of larger size, instead of minute cells provided with vibratile cilia, is rendered highly probable from the accounts given by Pringsheim respecting the fructification of *Œdogonium*, and from what I myself have also repeatedly noticed. Pringsheim discovers, in these various modes of

* A pre-existing aperture is certainly never found in this organ, either on its side or at its extremity. No one has ever asserted its existence; and Pringsheim's denial of it is therefore altogether superfluous. If Pringsheim has not seen the absorption of the contiguous cell-walls, it is either because his investigations have not been continued long enough, or because the species of plants examined by him do not present this mode of fertilization.

† See *Botanische Zeitung* 1860, p. 385.

reproduction, evidences of generic difference: I satisfied myself (in 1850) that they are only different varieties of the same act, and may occur in one and the same species, the form being determined by certain relative conditions of nutrition.

The knowledge of the fructifying process which takes place in the Algæ has been pre-eminently promoted by Thuret and Cohn, and of that which occurs in the higher Cryptogamia by Mettenius and Hoffmeister. In short, by the careful labours of these and of many other naturalists, it has been incontrovertibly established that, besides the multiplication of individual plants by buds or offsets—whether it be a single cell detached from the general mass, or a complex cell-mass, still forming part of the parent plant and developed from it (germ-granules or buds)—there is throughout all classes of the vegetable kingdom, with the exception indeed, at the present day, of the Fungi and Lichens alone, a sexual method of reproduction calculated to maintain the typical form of the species.

In fact, indications of a process of impregnation were seen, and its reality conjectured, by Ehrenberg in the Lichens and Fungi; and more recently, Itzigsohn and Rabenhorst, in the case of the Lichens, and Tulasne in that of the Fungi, have detected corpuscles to which they would assign the function of antherozoids.

I moreover observed a process of fructification in a Lichen, which will serve to establish the opinion that even in these simplest organisms a sexual act is performed. Of this observation I shall have to speak hereafter more at large. These various researches respecting the fructifying processes in the Cryptogamia make it at the same time evident that the mechanism of the proceeding—*i. e.* the nature and manner of the approximation of two heterogeneous cells, the union of which brings about the production of a new individual of a younger generation—varies so much the more as the structure of the vegetative organs is simpler. Whether the cell containing the fructifying material (pollen, antherozoids, spermatozoids, &c.) be provided or not with a locomotive organ, is of no importance in connexion with the impregnating act.

The assertions advanced, in opposition to the Linnæan doctrine, by Spallanzani, Henschel, Schelver, Bernhardi, and others, that the ovules of plants, as a normal condition, are stimulated by the pollen-grains to set up a new development of cells as the foundation of a fresh germ, and that moreover, in like manner, a new germ may be produced without the fructifying influence of the pollen on the ovules, are founded on inaccurate observations, and constitute the framework of hypotheses completely set aside by exact investigations.

Still, the propensity to credit what is marvellous, and to excite an interest by taking up the defence of bold hypotheses at variance with hitherto acknowledged laws, did not allow the results arrived at by the united assiduous labours of so many naturalists to go unchallenged.

For instance, a report made by Smith, in 1841, that he had noticed in the *Cœlebogyne* grown in Kew Gardens no male flowers, and that, notwithstanding this, the plant produced fertile seeds, induced Naudin to repeat Spallanzani's experiments on *Cannabis* and *Mercurialis*; and from the origination of fertile seeds in isolated female specimens of those two plants, as well as in a female *Bryonia dioica* grown in the open air, he felt himself entitled to deny that the fructification of the ovules of plants is necessary to the development of normal germs.

Radlkofer, prompted by the observations of Siebold (1857–1858) respecting the capacity of development of the unimpregnated eggs of bees and moths, made use of these statements of Naudin to construct his hypothesis of the parthenogenesis of plants; but, at the same time, he omitted to notice that the normal formation of buds and the development of ovules, occurring in an abnormal manner analogous to the production of buds, are long- and well-known phenomena, corresponding likewise with the production of living progeny by the Aphides and Trematoda, and with that of barren eggs by insects.

Under the influence of his preconceived ideas he has failed to note that the researches of Naudin were instituted on polygamous plants,—a circumstance which naturally suggests to the mind that a concealed male flower, or an anther produced in the interior of a female flower, may have led the observer into error.

The observations of Smith on *Cœlebogyne* appeared to Radlkofer's mind to supply ample evidence in favour of his notion of vegetable parthenogenesis. Some examinations were undertaken by him on the *Cœlebogyne* and its embryos during a visit to Kew, in the course of which he once detected a pollen-cell on the stigma; this occurrence, however, failed to shake his faith in the conclusion he had already arrived at.

The same fortune that befell Radlkofer also attended Braun, who in the same year got Deeke to examine the embryos of the *Cœlebogyne* cultivated in the Botanical Gardens of Berlin. For although Deeke showed that there is a normal act of fertilization of the germ-vesicles in the embryo-sac of *Cœlebogyne*, yet Braun considered himself justified in propounding to the Berlin Academy his ideas of parthenogenesis in plants. Braun further supported this hypothesis by appealing to the before-quoted researches of Henschel and earlier inquirers, and to the circumstance of the much rarer existence of male specimens of *Chara crinita*, to which he thereupon attributes, without further research, a parthenogenetic mode of reproduction.

That the investigations, repeated by Naudin, of the development of unfertilized ovules in *Cannabis* and *Mercurialis*, and likewise the older experiments by Spallanzani, Lecoq, and others, asserting the same development to occur in the ovules of *Spinacia*, are untrustworthy, follows as a consequence of the researches undertaken by Regel and Schenk. On the one hand, Regel always detected male among the female flowers on the same plant; on the other, it follows (in accordance with the rule) from Schenk's admirable experiments, that the notion of the formation of fertile seeds without the operation of pollen upon the ovules of a plant, is not established. Both observers concur in saying that, of all the plants adduced as parthenogenetic, the *Cœlebogyne*, which was not accessible to them for investigation, forms the only exception to the general law, and that ovules become fertile seeds only after the act of fertilization. Schenk was led to believe in the existence of the exception mentioned, inasmuch as he relied upon the authority of Braun, who made it appear that he had for a long time examined the *Cœlebogyne* with the most scrupulous care in his room; but Regel formed a more unbiassed opinion, and gave to the unsupported statements of Braun and Radlkofer no such implicit belief.

Both these careful observers would have convinced themselves with ease of the groundlessness of the hypothesis of Radlkofer and Braun, if they had been enabled to examine a plant of *Cœlebogyne* in bloom.

The delusion of the two last-named observers, that they were able to make out, from among the structures of the normally-formed male flowers, the impossibility of the presence of a hermaphrodite flower in *Cœlebogyne*, rendered them blind to the existence of the comparatively large anthers, which, in fact, are often developed at the base of the calyx of the female flowers, as I have had opportunities of observing for two years in the specimens growing in the Berlin Botanic Garden.

That Radlkofer did not discover the hermaphrodite flowers of *Cœlebogyne* is attributable to the hasty character of his observations during his travels; but this, if in the least explicatory of the circumstance, is no apology for it. The finding of pollen on the stigma ought to have rendered him cautious, had he been only anxious for the discovery of the truth, and not, as is clearly the case, for the promotion of a literary work by the fallacious evidence of a preconceived interpretation. But that Braun, after several years' observation of the plant in question *, and after

* Whilst this sheet was passing through the press, I received from Prof. Braun his just-published "Supplement to the Treatise on Parthenogenesis

he had been shown by Deeke the fructifying pollen-tube in the embryo-sac, should not be acquainted with the fact that during the entire summer, from the beginning of May till the end of August, hermaphrodite flowers are not rarely met with on *Cœlebogyne,* is altogether incomprehensible.

Cœlebogyne (Smith).

The hermaphrodite flowers observed on the *C. ilicifolia* from May to August, in the Berlin Botanic Garden, were all monandrian. The single anther developed (Pl. X.) was situated on the periphery of the flower; it alternated on the outer aspect with the inferior first and with the adjoining fourth leaf of the calyx, and on the inner aspect with two of the carpels. Sometimes a second aborted anther is met with, also alternating with two carpels and situated opposite the third leaflet of the calyx. The stamens are attached to the bottom of the flower. The perfect one is equal to the sepals in length, and consists of a cylindrical, thick, fleshy filament, at first erect, but afterwards curved outwards; it gradually expands upwards to the 'connective,' which is free on the exterior; to this last is affixed an oval, reniform, orange-coloured anther-cell, having a discharging slit-like outlet prolonged to its apex. Though the anther has two parallel compartments when first formed, the septum breaks down between them at a very early period of development, when the entire stamen is still concealed within the calyx and the pollen is completely undeveloped.

Braun, who had the opportunity of examining some portions of a male flower which had been preserved in the Herbarium at Kew, as belonging to *Cœlebogyne,* describes the anther-cell to be "elongated, consisting of two halves, in contact above and below, but rather separated at the centre by the 'connective;' strongly curved on the outer aspect, where likewise the elongated slits for dehiscence are placed." This description of the anther of *Cœlebogyne* from Hooker's collection might raise the doubt whether the male organs described by Braun actually belonged to *C. ilicifolia,* were it not that, very fortunately, the most important contradictions in the account given by Braun to what I observed in the specimens obtained from the Botanic Garden of Berlin, particularly in respect to the variation in the form of the anthers, are removed by the illustrations that Braun has appended to his own essay. For instance, Braun says the anther-

in Plants—Polyembryony and Germination of *Cœlebogyne*" (extracted from the Transactions of the Berlin Academy for 1859, printed in 1860). In this work Braun adduces (p. 197) further evidence in illustration of parthenogenesis, without, however, assigning any great importance to it. But *Cœlebogyne* still constitutes, as heretofore, the mainstay of the doctrine of the parthenogenesis of plants.

cell is elongated, oblong, whilst I feel obliged to call it oval if I indicate its form according to the principles of nomenclature given by Linnæus and employed by the best authors, and as, moreover, it is in fact represented by Braun*. Moreover the mode of attachment of the anther to the filament, as described by Braun, differs from what I have found and represented; for he says the filament is very short, and affixed in a joint-like manner to the inner side of the connective. If this relation of the parts be true, and not an error in description, like that above noticed of "elongated, oblong," the cause of this assertion of Braun would in truth appear to be that the male organs examined could not have been those of *C. ilicifolia* of the Gardens of Kew and Berlin: for no example of a species is known to me having both those modes of attachment of the anther on the filament severally described by myself and Braun; in short, according to the prevailing notions of generic characters, plants so formed would belong to two distinct genera.

Since I have not had the opportunity of examining the male flowers of *Cœlebogyne* from Hooker's herbarium, I am unable to decide this point; we must therefore wait until Hooker, or some botanist familiar with the morphology of plants and with these particular inquiries, can give us an account of the true state of the case †.

This doubt, whether the male flowers of *Cœlebogyne* examined by Braun and myself were equivalent, would necessarily extend to the further account given by Braun of the female flowers of this plant, had I not thoroughly assured myself that I had the same individual specimens before me that Braun himself investigated, —a fact which does not appear, even in the case of the female flowers, from the descriptions of them given by Braun, but rather the contrary.

Thus, Braun describes the calyx of the female flower of the *Cœlebogyne* of the Berlin Botanic Garden to be deeply five-cleft (quinquepartitus), and rarely four-cleft (quadripartitus), whereas I, on the contrary, found the calyx to consist of five completely-separated, distinct sepals, imbricated in vernation; the leaflets never coalesced (gamosepalous), five-cleft (quinque-partitus), nor lobed, as Braun further terms it in his German description. Moreover in the same place he speaks of the

* The long diameter of the anther is not double its transverse diameter, and it is rounded, not pointed,—wherefore we must call it oval, according to Linnæus (Philosophia Bot. 1751, p. 42), Willdenow (Grundriss der Kräuterkunde, p. 78), and Bischoff (Handbuch der bot. Terminologie und Systemkunde, p. 74).

† I am, however, convinced that Braun's faulty description has alone given rise to this doubt; Decaisne (*Ann. des Sciences Naturelles*, vol. vii. 1857) has already corrected Braun's statement on this point.

leaflets of the calyx—a mode of expression not usual with botanists in the description of plants, except where the calyx consists of a whorl of free and non-united leaf-like organs or sepals.

Further, the form of the stigma is described in an anomalous way by Braun: the lobes are not "somewhat emarginate at their extremity (lobis expansis integris subemarginatis)," but each of them has several dentations along its upper edge, more or less deep, and three or four marginal teeth, or more seldom two such; and the edge is very rarely entire. This therefore is clear, that Braun selected an imperfectly developed bud, and described its condition as the rule, instead of a fully-developed flower,—a circumstance it is always necessary to have stated. The correctness of this conclusion is manifest from Braun's description of the position of the stigmas; for he says they arch over and are compressed against the capsule, whereas in the developed, full-blown flower the stigmata are horizontal and somewhat erect.

At the base of the external whorl of sepals, and partly adherent to the short axis of the flower, several glands are met with, usually one on each side of every sepal, of tolerably large size, hemispherical, and flattened at their apex. A fifth similar gland is also frequently found at the base of the free border of the third leaflet of the calyx.

Braun, again, is incorrect in his ideas respecting the attachment of the flowers, since he says, "Several female flowers grouped together at the extremities of the pedicels constitute strictly called few-flowered, apparently loose spikes. These are provided with a terminal flower, which is formed at an earlier period than the lateral blossoms, of which latter the upper slowly succeed the lower in the order of inflorescence."

The flowers, including the lateral ones, are, however, not sessile, as Braun implies, but shortly stalked, as Smith indeed rightly described them, and are situated in the axis of a bract; their pedicels are furnished with two bracts, similar to the leaflets of the calyx, and usually support a gland on each side of their base.

The presence of the bracts on the pedicels of the flowers, and the earlier expansion of the terminal than of the lateral flowers, afford unequivocal evidence that the mode of inflorescence we have here cannot be strictly named "a few-flowered spike," but is nothing else than a few-flowered "cyme" the lateral flowers of which are so shortly stalked that the whole inflorescence acquires a spike-like form, or constitutes a *cyma spiciformis*.

The description of *C. ilicifolia* given by Braun is not, indeed, sufficient to establish the identity between the species examined by him and by myself: however, I am thoroughly convinced of the fact of this being the case; for, as Braun himself states, only three flowering plants of *C. ilicifolia* existed in the Berlin Botanical Garden, and two of the self-same examined by him I also had the opportunity of investigating.

Thus it appears that the last insecure prop to the hypothesis of parthenogenesis in plants is thrust aside, and it is established beyond doubt that the production of a normal germ in the female organs is dependent upon the cooperation of the male organs of plants.

The Pollen.

The pollen escaped from the anthers of *Cœlebogyne* is spherical, and composed of a very delicate smooth integument enclosing fluid contents. The external coat is remarkable in having three symmetrically-disposed darker or clearer specks on its surface. The fluid contents have suspended in them a multitude of oval and rounded firm corpuscles, which are coloured partly blue and partly yellow by iodine.

The different transparency of the three points alluded to in the wall of the pollen is due either to the presence of small globular (collenchymatous) corpuscles, or to the detachment of such cells, and the consequent production, by the spaces left in the coat where they adhered, of clear circular specks with a dark outline. The internal very delicate pollen-coat, which cannot be distinguished from the outer tunic except after the application of chemical reagents, becomes evident at these clear spaces when the pollen-cell proceeds to elongate itself on the stigma (Pl. X.).

The pollen-grains (united in groups of four) contained within the half-developed anther-cell possess thicker coats, and on that account completely occupy the mother-cells in the parenchyma, of which four are formed in each anther-cell. The special mother-cells are very manifest, and are thickened during the whole period of the deliquescence of their parent-cell, and present the appearance of "imperfect" parenchyma-cells (collenchyma) (Pl. X.).

These cells enclose four others of a second generation, one of which, the intine of the future pollen-grain, at this period almost entirely fills up the parent-cell, and contains a uniformly thick mucoid fluid, whilst the other three grow to a very trifling extent, and are so compressed by their largely-developed fellow-corpuscle against the wall of the mother-cell, that they come to occupy a position between the two coats of the pollen-cell—the extine and the intine.

They are the "intermediate corpuscles," described by Fritsche as having a similar situation in the cell-structure of all varieties of pollen, and without doubt owe their origin to the same cause which gives rise to the circumstance that the vesicles* which cha-

* I frequently call the non-nucleated cells, which commonly perform a secretory function (H. Karsten, De Cella Vitali, 1843, p. 64), for brevity's

racterize porous parenchymatous cells and vessels always correspond to each other in the adjoining walls.

In the course of the further generation of the pollen-cells the soft mother-cell becomes progressively absorbed, until it is reduced to a most delicate and scarcely perceptible membrane, as we find it to be in the mature pollen-cell at the time of impregnation, and when at length it is broken through by the agency of the three vesicles distended by the absorption of fluid. In this way the openings (pores) originate, in the vicinity of which the intine begins to extrude.

At the time of the separation of the little-cells from the mother-cells of the *Cœlebogyne* (which in their origin stand related, like the dotted cells of wood, to the peculiar porous cells, and which ought therefore rightly to be called, not porous, but dotted cells), they can scarcely be recognized as such; for their walls are so thick, that their cavities are, like those of starch-grains, extremely contracted. Since Fritsche's observations on pollen, we know that the "intermediate corpuscles" existing in fully-developed pollen may not rarely be recognized as actual cells. I represented, in my 'Flora Columbiæ,' vol. i. pl. 44, the pollen of *Schachtea*, which also displays very clearly this same relative structure. The intermediate corpuscles, distinctly recognizable as vesicles, occupy, as do those in *Cœlebogyne*, the same position as the "opercula" of Fritsche, and are thrust aside by the expanding intine: until this period they constituted the "porous canal" in the wall of the extine.

The length of this canal necessarily depends in part upon the thickness of the extine of the pollen, and in part on the dimensions of the cell which constitutes the intermediate body. In *Cœlebogyne* the canal is exceedingly short; in *Œnothera* and *Clarkia** its development is very considerable, and both the cell concerned in its formation is very large, and the outer portion of the distinct canal hollowed out in the highly thickened extine of considerable length.

How essential the developmental history of organic bodies is to the correct apprehension of structural relations is exemplified by Schacht's most recent work on this subject of pollen-structure; for, notwithstanding his marvellous skill in the representation

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sake, vesicles. A superfluous and incorrect designation for these structures is the expression '*vacuoles*.'

* In *Clarkia pulchella* the wall of the intermediate cell is intimately united with the intine and extine on either side of it, whilst these two membranes are not in union, so that on a transverse section a fissure appears between them, as Schacht has figured ('Physiologie,' pl. 10. fig. 17), and as he states may be demonstrated very clearly in half-developed pollen-granules of this species.

of the transverse section of the mature pollen of *Clarkia*, as well as, indeed, of *Cucurbita* and other plants whose pollen is provided with intermediate corpuscles, he is so entirely mistaken with respect to its nature that he attributes the condition to thickening of the inner pollen-coat.

That these "dot-cells" of *Cœlebogyne* and allied forms, together with the cells containing the fovilla, are, in relation to the extine, cells of the second generation, can be made out only by their developmental history. For, in fact, they mostly retain within the pollen-cell, during the first stage of development, the appearance of secretory cells; still it is rare that they contain secretions, as happens in *Onagraria* and *Geranium*.

Their function evidently is, either by means of the osmotic action of their contents, or by the transformation into mucus and the consequent swelling-up of their enveloping membrane, to cause the rupture of the extine, which is always very thin above them. Then they in their turn are thrust out or absorbed by the outgrowing intine, to make way for its extrusion.

Without doubt similar cells are in requisition in all cases (as Fritsche indeed surmised) to effect the perforation of the extine, when the ripe pollen comes into contact with the moisture of the stigma or any other appropriate fluid.

Besides these cells, which originally held the same genetic position as the "intine," there exist very frequently, within the fluid contents of the pre-formed (parental) sac of the *extine*, some actually secreting-cells, containing volatile oils and other secreted matters. These vesicles especially contribute to produce the great varieties in the external aspect of pollen, either being so modified in growth as to constitute warts or spines on the surface of the extine, which is usually in part simultaneously absorbed, and in part transformed into lignine, or so spread out uniformly over the whole surface of the pollen-grains, except where these are in mutual contact, as to form a sort of epidermal covering over the intine.

In pollen-grains furnished with folds, the involutions of the extine have no such cellular membrane on their surface. Also in porous pollen-grains, where the pores of the extine are in part due to the presence of "dot-cells," there is not unfrequently an unusual number of them, developed by endogenous growth, which again by their manifold transformations still further multiply the varieties of pollen.

Mohl, indeed, in his standard work on Pollen (1834), expressed the opinion that "the outer integument of the pollen must be regarded as a structure composed of cells or of their rudiments and of a homogeneous connective tissue."

Unfortunately this distinguished histologist, misled by the result (not entirely borne out by facts) of later investigations of the cuticle, has, in a new exposition of the structural relations of the pollen, expressed himself somewhat ambiguously respecting them, and in such a way that his description has tended to strengthen the prevailing erroneous hypothesis, that the outer lamina of the epidermis (the cuticle) is produced from the subjacent layer by a process of secretion or exudation.

This theory of the growth of the cell by a simple act of deposition or exudation, after having prevailed during the last generation, must certainly be exploded; for it is contradicted by the progress of physiology. For though I was not able to disprove it by the facts presented in my dissertation (De Cella Vitali, 1843) and in other works, yet my repeatedly adduced demonstrations respecting the origin of resin and of the wax-like cuticular lamina of plants must convince every thinking person that organization is not a mechanical but a dynamical or vital act. (See 'Botanische Zeitung,' 1857, p. 313, and Poggendorff's 'Annalen,' 1860, p. 640.)

That the "dot-cells" which lie on the inner wall of the extine, and at a later period effect its perforation, may produce a secondary generation of cells, has just been remarked; and the same phenomenon is also sometimes observed in the case of the porous ligneous cells of the Coniferæ. This circumstance is very clearly illustrated by me, in the fourth plate of the 'Flora Columbiæ,' in the figure of the pollen of a *Bignonia*, the membrane of which is occupied by a large number of small, not quite flat, oval cells, not in contact with each other. Further, each of these contains a third generation of smaller cells, about sixteen in number, and together form an envelope around the smooth enclosed intine. After being macerated for a time in dilute sulphuric acid, the cells of the second generation detach themselves from their parent-cell, to the inner surface of which they were affixed, and are seen floating freely about under the object-glass. The membranes of these different generations of cells are in this case not thickened: were they so, we should have such forms produced as are met with in Synanthereæ, Nyctagineæ, Convolvulaceæ, &c., except that, in these, the cells of the second and subsequent generations become frequently converted into setæ, which project from the whole external surface of the extine, and are therein analogous to what is so clearly demonstrable in the hairs of the epidermis. Moreover, the structure of the spores of Cryptogamia, so thoroughly investigated by Mohl, teaches us very distinctly the signification of the reticulated surface of these bodies, so nearly allied to pollen-grains, in all that relates to their mode of development. This assertion is especially corroborated in the case of the spores of Acrostichaceæ, Ascleniaceæ, and Aspidiaceæ, some of which I figured in my 'Flora Columbiæ' (I beg to refer particularly to plates 52 and 57). The endogenous cells, which here clothe the extine as a completely closed membranous layer, are in these spores, as also in almost all others, not entirely flattened, but resemble the "dot-cells" (the intermediate corpuscles of Fritsche), and are, in the groups named, polyhedral, and in many others globular in form. When they contain no younger generation of cells, it is so much the more a problem whether they belong to the series of "dot-cells" or of "pore-vesicles;" but this is a matter of no consequence for the understanding of their anatomical structure. Those spores enveloped by cells are particularly interesting on account of the subsequent development of a sort of setæ, which, as their age increases, cover their surface, and entirely differ from those which derive their origin from a peripheral elongation of the porous vesicles. Further development takes place only in those walls of the cells forming the outer surface of the spores which lie next the intine and are in contact with each other (being in this respect somewhat similar to the cells of the sporangial ring and to the parenchyma-cells enveloping the vascular bundle of the Fern),—mostly, indeed, only where the three cells touch; for they are not completely in apposition. The extine itself and the superposed peripheral wall of endogenous cells are not thickened, but on the contrary are destroyed, in the older spores, so that only the thickened angles and walls are left behind, setiform and spike-like.

Similar structures are also found among the pollen of Phanerogamia, *i. e.* in *Cobæa scandens*, as Mohl has tolerably well pointed out. On the contrary, Fritsche and Schacht question whether the cellular reticulated envelope of the exterior of these pollen-grains is composed of actual cells; for, according to their views respecting the growth of the cell-wall, this external wall originates from the exudation and deposit of matters which, from some inconceivable reason, take on this wonderful reticulation. The study of the progressive development of these pollen-grains at once overturns this fantastic idea, and renders it easy to understand that the cells which are formed between the extine and intine, and construct a complete layer between the two, become lignified in the same manner as has been described in the spores of the Polypodiaceæ; only that, in addition, those cells in mutual contact become thickened and porous, and combine to form a series of radiating pores.

This cellular external tunic of Fern-spores often breaks up into its three component portions, which are divided from each other by stronger, thicker walls; and from all this we gather that the cellular envelope of the smooth intine of the Ferns is composed of three cells coating the very delicate, transient extine of the spores: these cells entirely occupy the intermediate space between the two membranes, and each of them contains numerous endogenous cells.

This fact of the breaking up of the integument of the Fern-spores into three segments recalls our attention to similarly constructed pollen-grains, namely, to those in which the openings in the extine are furnished with opercula, which are either simple or cellular, smooth or setaceous.

Three cell-like opercula, which occupy the whole circumference of the pollen, are found in many Passifloreæ; smaller ones, in greater number, beset with setæ, belong to many other species of this family, as well as to many Cucurbitaceæ, &c. In the Cucurbitaceæ, the opercula, besides being covered with setaceous enlarged secretory cells belonging to the extine, are in their formation evidently dependent on the "dot-cell" (intermediate corpuscle) adjoining each operculum; and in the Passifloreæ it is most probable that the very large "intermediate corpuscle" actually constitutes the operculum.

In the 51st plate of my 'Flora Columbiæ,' I figured the pollen of *Passiflora servitensis*, with its three very large opercula, attached to the stigma in the act of protruding the intine. This pollen shows that the different layers which Fritsche first observed on the intine are not always laminæ of one and the same cell-membrane, and that the actual intine is not always a cell of the second generation, but may, in fact, be one of the third.

Betwixt the two laminæ which hitherto have been together regarded as the intine, a small "dot-cell" is observed, as in the pollen of many Monocotylæ, whilst three such are met with in the pollen of *Cœlebogyne* and of most Dicotylæ. Two sorts of cells are thus formed in the extine, from one of which the fovilla is separated, whilst the other appears intended to facilitate the expulsion of the sister-cell from the mother-cell. From the researches of Meyen and Schacht it also seems evident that the pollen of Coniferæ belongs to this category.

It remains for future investigators to consider this relation of the parts of pollen, and to decide, with regard to the different forms of pollen, whether the opercula are immediately derived from the "dot-cells," or from a portion of the extine as a consequence of the contact of this with the "dot-cells." Both forms are met with. That the "porous vesicles," which are frequently charged with secretions, as well as the "dot-cells" may be transformed directly into opercula, is not improbable; nevertheless opercula do also originate independently of these cell-structures in the extine, the position and size of which are determined by the contiguous "dot-cells," as for example in the Cucurbitaceæ, where the "dot-cell" (the "intermediate corpuscle" of Fritsche) does not appertain to the intine as a thickened lamina, as Schacht implies, but from the first lies free between the two coats of the pollen, and at a later period becomes strongly attached to the extine. Consequently it clings to the extine when this is torn from the intine and gets so inverted that its setaceous outer surface is turned inwards.

The pollen-cells of *Thunbergia*, with their thickened extine disposed in spiral lines, remind us at once of the spiral-fibres of the vessels of Cryptogamia, and represent a modification of the spores of Equisetæ; whilst the pollen of *Ipomœa*, with its setaceous integument, may be considered like ligneous *Vaucheria* zoospores, as is proved by my history of the development of the latter (Botan. Zeitung, 1852, p. 95, pl. 2. fig. 12 *a*).

Each cilium of the vibratile epithelium of the zoospores of *Vaucheria*, and likewise the cilia of the cells of antherozoids and spiral fibres, are vesicles, which in the course of development assume a hair-like form, and it is most probable move the body to which they are attached, both by the agency of a great faculty of imbibition in their unequally thickened walls, and by great efforts in the diffusion of their contents with water—actions which proceed for some time with oscillating movements before an equilibrium is attained.

It can only be want of knowledge of the developmental history of these cells that can suggest the opinion that cilia are direct outgrowths of the primordial vesicle.

[To be continued.]

X.—*On Additions to the Madeiran Coleoptera.*

By T. Vernon Wollaston, M.A., F.L.S.

Fam. **Dytiscidæ.**

Genus Eunectes.

Erichson, Gen. Dytic. 23 (1832).

Eunectes subcoriaceus, n. sp.

E. oblongo-ovatus, subdiaphano-coriaceus, pallide diluto-testaceus, clypeo antice leviter emarginato; capite postice nigro et macula frontali magna distincta antice profunde bipartita ornato; prothorace vitta transversa parva fracta nebuloso, ad latera oblique subrecto, angulis posticis acutiusculis, subæquali, margine postico infra angulos leviter elevato; scutello subsemicirculari; elytris punctis magnis triplici serie et punctulis minoribus parvis (anterius minutis levioribus et magis remotis) nigris notatis, utroque macula